

BRACHYGNATHIA IN DAIRY CATTLE

by

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B. S., Kansas State University, 1959

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Dairy Science

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1963

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INTRODUCTION

One goal of breeders of purebred dairy cattle is to raise cattle that meet the requirements of their respective breed organizations and conform closely to the model cow in that particular breed. Because of this, they are particularly interested in the inheritance of any defect which will keep them from attaining this goal. If the mode of inheritance of a defect is known, the defect can be controlled at small frequencies or at least reduced in frequency through the use of a suitable breeding program.

In the show ring, skeletal deformities have been of interest for many years. A number of these conformation defects are of enough importance or frequency that they are listed on the Purebred Dairy Cattle Scorecard. This study is concerned with one of these defects: brachygnathia. The defect has many common names. Among them are parrot-jaw, short-jaw, pig jaw, and over-shot jaw. On the Purebred Dairy Cattle Scorecard, parrot-jaw carries the penalty of slight to serious discrimination.

Other than the discrimination in the show ring, the parrot-jaw defect does not affect the animal adversely, except in cases so severe as to hinder the prehension of feed. However, animals affected this severely are quite rare. Of course, if the defect should interfere with eating, this will in turn affect the condition and milk production of the animal. The defect does not appear to have any side effects which reduce the animal's value as a milk producer.

Although some work concerning abnormalities of the jaws has been done in various species, very little is known of the inheritance or the morphology of this defect in cattle.

This study has been conducted with two major objectives in mind. The first is to determine the inheritance of the parrot-jaw condition. This has

been done through the study and analysis of results of breeding trials in an experimental herd and elsewhere. The second objective is to define the defect morphologically and anatomically. Heads from both parrot-jaw and normal slaughtered animals were measured to determine which bone or bones were involved in the expression of the condition. Measurements have been taken also on live animals, both normal and affected, for the same purpose.

REVIEW OF LITERATURE

Occurrence and Inheritance in Other Species

Brachygnathia, or overshot jaw, has been observed in several species. Some of these are dogs, cattle, mice, guinea pigs, and sheep.

Stockard, in his studies with dogs, concludes that the characteristics of the upper and lower jaws are inherited and may develop independently of each other (13). Because of this independence, four types of development can result: one where both jaws are normal; a second where both are long, but still have normal occlusion; and two types where the jaws vary in opposite directions, resulting in malocclusions.

Grüneberg and Lea attributed an overshot condition in long-haired Dachshunds to an autosomal recessive gene (4). Phillips concluded that mandibular shortening in Cocker Spaniels probably is inherited as a recessive with multiple modifying factors (9). Only the most pronounced "pig jaws" could be detected at birth. Some pups did not show the defect until after weaning. Since all pups were sold at weaning time, they could not be traced to check on the overshot condition. Maximum shortening appeared to be incompatible with life.

Mordby and others have done considerable work on the jaw abnormalities

in sheep (8). They found the overshot condition was not as simply inherited in sheep as in the Dachshunds observed by Grüneberg and Lea. Their evidence eliminated one or more pairs of recessive genes as the sole cause of the defect. They stated that some of the genes were certainly dominant and additional recessive genes could be involved. They concluded that the defect might have resulted from interactions among several pairs of genes.

The overshot condition was one of the lesser grades of otocephaly reported in guinea pigs by Wright (14).

Micrognathia is a condition in humans, in which the lower jaw is short (1). Little is known of the etiology or morphology of this condition.

Occurrence and Inheritance in Cattle

The inheritance of parrot-jaw in a herd of Jersey cattle has been studied by Huston (6). A simple recessive mode of inheritance was postulated. He analyzed the pedigrees and the results of 82 matings, eight of which produced parrot-jaw offspring. The probabilities obtained were such that the original single gene recessive hypothesis could not be rejected.

In a preliminary report of the data in this study, Smith et al. stated that the results of Guernsey-Jersey crosses could be explained by simple recessive inheritance (10). P. Koch started some breeding trials at the Berlin Animal Breeding Institute (7). The mating of two animals showing the short-jaw defect produced a normal calf. The mating of this same bull with a parrot-jaw cow of another breed resulted in a short-jaw calf. Koch concluded that this was proof of the heritability of brachygnathia, but no conclusions can be made concerning the mode of inheritance.

Hancock observed a short lower jaw condition in New Zealand cattle and emphasized its importance from the standpoint of being a hinderance to grazing

animals (5). In that study a female with the short-jaw defect grazing on short turf produced only 100 pounds of butterfat in a year. Normal animals on the same pasture produced 360 pounds. He supposed that the length and shape of the lower jaw was controlled by hereditary factors, because he observed the defect in both of a set of identical twins. Hancock believed, however, that environmental factors could influence embryonic development because the degree of shortness was not the same in the twins.

Morphology and Anatomy

Stockard concluded that the modifications in the palate and the maxilla were more responsible for dental malocclusions than were changes in the width-length relations of the mandible (13). He concluded from his studies that, in dogs, dental malocclusion resulting from mandibular deformity is largely secondary.

Nordby and others found that the upper jaw of overshot sheep was longer than normal while the mandible was shorter than normal (8). The maxilla of affected ewes averaged 12% longer than that of normals. They found that the mandibles of overshot ewes averaged 18% less than the mandibles of normal control ewes. Their measurements showed that the anterior parts of the mandible were affected more than the rest of the mandible.

Grüneberg and Lea found, as did Nordby et al, that the anomaly of the overshot animals concerns the anterior parts of the jaws rather than the jaws as a whole (4). They found the occlusion in the regions of the carnassials and the molars to be entirely normal, both in living animals and skulls.

Grüneberg and Lea determined that the faulty occlusion of the front teeth was caused by both a shortening of the mandible and a lengthening of the upper jaw, at least in fully grown animals. They concluded from information obtained

from radiographs that the mandible was primarily affected, and that the alterations in the upper jaw were of secondary nature. This view conflicted somewhat with the conclusions of Stockard.

Grüneberg and Lea further postulated that the mandible was primarily affected. This led to an occlusion of the lower canines behind, rather than in front of, the upper canines. The pressure exerted by the lower canines caused an elongation of the anterior parts of the upper jaw.

Donald and Wiener noted that brachygnathia was not always caused by a shortening of the mandible, but may have been due to a lengthening of the upper jaw (3). However, they stated that more extensive comparative measurements must be made to determine whether the upper jaw is long and the lower jaw normal or whether the lower jaw is short and the upper jaw normal.

METHODS AND PROCEDURES

Definition of the Condition

Brachygnathia is defined as "the state of having an abnormally short lower jaw". Likewise the term "overshot" is taken to mean that the lower jaw is too long. Such definitions describe the conditions adequately but imply that the defects are limited to the lower jaw or mandible. Such statements as these cannot be made in the light of present day knowledge.

In this study, brachygnathia was considered as the condition where the lower incisors meet posterior to the dental pad. The malocclusion in the animals observed ranged from cases where the teeth met immediately posterior to the dental papilla to those where the incisors met on the 4th dental ridge. In most instances the incisor teeth met between the 1st and 2nd dental ridges, making them $1-1\frac{1}{2}$ inches posterior to the dental pad. The malocclusion of

affected animals can be seen in figure 1. Any animal whose incisors met on the dental pad was considered normal.

Figure 1. A) A parrot-jaw Jersey female.
B) A parrot-jaw Guernsey female showing the incisor teeth meeting near the 1st dental ridge.



Parrot-jaw has been observed in four major dairy breeds: Jersey, Guernsey, Holstein, and Brown Swiss. Field reports indicate that the occurrence of the condition is of greater frequency in the Jersey and Guernsey breeds.

From observations of parrot-jaw animals in the different breeds, there appear to be two types of abnormality. These two types of parrot-jaw appear different phenotypically. The heads of Guernsey, Holstein, and Brown Swiss parrot-jaw animals appeared to be long and narrow. When the defect was observed in Jerseys, the head did not seem to be long but rather the jaw appeared weak. Pictures of affected animals of each of these breeds can be seen

in figures 2, 3, 4, 5, 6 and 7. The type observed in the Jersey breed may appear normal at birth and malocclusion occur later in life. This is similar to the 'pig jaw' in Cocker Spaniels reported by Phillips (9). The other type of parrot-jaw is short when the animal is born and remains so throughout life. The incisor teeth meet at the same point all through life as they do at birth. The degree of shortness does not appear to increase with age. This type does not become shorter as the animal grows as is the case with the first condition mentioned.

Nature of Breeding Investigations

Since 1950, a small breeding herd has been maintained at Kansas State University for the study of brachygnathia. The herd was founded with 1 parrot-jaw Guernsey bull, 3 parrot-jaw Guernsey cows, 3 parrot-jaw Jersey cows and a normal Jersey bull that was known to sire short-jaw calves.

Matings in the experimental Guernsey herd have been carried on for four generations. The females have been backcrossed to affected Guernsey sires except for a short period after the first herd sire died when no parrot-jaw bull was available. During this period, the herd was bred artificially to normal Guernsey bulls.

The Guernsey bulls were mated to the parrot-jaw Jersey cows and a cross-bred herd established. This crossbred herd is presently in the third generation. As was the case in the Guernsey herd, all females were backcrossed to parrot-jaw Guernsey bulls, except during the time when no bull was available for service.

A few matings were made with an affected Brown Swiss bull and two short-jaw Brown Swiss cows from the Garden City Branch Experiment Station.

Matings were also made between a parrot-jaw Holstein female and Guernsey



Figure 2. Side view of a Holstein parrot-jaw.



Figure 3. Side view of a Brown Swiss parrot-jaw.



Figure 4. Side view of a Guernsey parrot-jaw.



Figure 5. Side view of a Jersey parrot-jaw.



Figure 6. Lateral view of a Guernsey parrot-jaw.



Figure 7. Ventral view of a Guernsey parrot-jaw.

bulls but death of the calves and sterility of the cow prevented the founding of a Guernsey-Holstein herd.

The matings in this experimental herd have involved more than eighty animals.

Nature of Genetic Analyses

The analysis of the inheritance of any condition in large domestic animals is beset with a number of problems. Not the least of these is the long generation interval and the small number of offspring per animal in a lifetime. Enough observations to arrive at a definite conclusion from any kind of matings are difficult to obtain.

As Stockard concluded, variations in the upper and lower jaws can lead to four types of development (13). The types which have normal occlusion are of no interest in this study. The type of variation of concern in this study is that where the lower jaw meets posterior to the upper jaw, thus resulting in malocclusion.

One major question in this regard has been proposed by Donald and Wiener (3). Is the defect caused by a normal upper jaw and a short mandible or is it caused by a normal mandible and a long upper jaw? Another possibility could be: is it a combination of the two conditions? One could conceive a situation where the variation of either jaw by itself would be so slight as to pass unnoticed. Only in cases where both jaws vary in opposite directions would it be possible to observe the defect.

If the characteristics of the upper and lower jaws are inherited independently, a change in one of these might indicate a simple mode of inheritance. On the other hand, if both jaws vary in opposite directions, this would suggest a more complex inheritance with several genes interacting.

In this study an attempt was made to explain the inheritance as simply as possible. Inherited defects occur as the result of gene mutations. Most abnormalities can be explained by the mutation of a single gene. The simple hypotheses are tested first because they involve events that have a greater chance of occurrence. The most simple hypothesis is accepted unless it can be proven false. When the more simple hypotheses are discarded, then alternatives are considered.

The hypotheses are tested by comparing the probability of occurrence of the phenotypic ratios observed in the offspring of a group of matings with the ratios expected under the proposed genetic hypothesis. However, with so few matings of each kind, and some cases where it is hard to assign a genotype to the parents, these tests cannot be very powerful.

Nature of Morphological Analyses

The second aim of this study was to determine morphological and anatomical differences between parrot-jaw and normal animals. Three sources of data were used in doing this.

Measurements were taken on 255 Registered Guernsey females from eight dairy farms. These females ranged in age from 3 days to 14 years. The measurement values obtained were analyzed and regression lines established. With this information, the expected measurement value for a normal animal of any given age was estimated by the use of the prediction equation, $\hat{Y} = \bar{y} + b(X - \bar{X})$. The parrot-jaw Guernsey females in the experimental herd were measured at several different ages. These values were compared with appropriate normal control figures obtained from the prediction equation.

Whenever an animal left the Kansas State University Dairy Genetics project herd, its head was kept for further measurement. One set of measurements

was taken of the head when it was freshly butcher-skinned. The head was then macerated and the skull and mandible bones measured. Other Guernsey heads from the University herd also were obtained to serve as controls. Measurements from parrot-jaw heads were compared then with the values obtained from normal control heads.

RESULTS AND DISCUSSION

Inheritance

Introduction. Evidence concerning the inheritance of the parrot-jaw condition has come from several sources. Experimental matings in the Kansas State University Dairy Genetics project herd were made in the Jersey, Guernsey, and the Brown Swiss breeds and in Guernsey-Jersey and Guernsey-Holstein crosses. Other information has come from the Kansas State University Jersey herd where three parrot-jaw cows were observed. Still other information came from field cases in the state. All this information was analyzed in attempting to determine the mode of inheritance that best would explain the occurrence of the defect in these breeds and breed crosses.

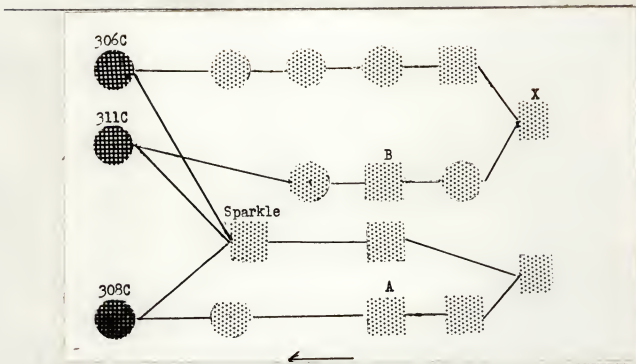
Frequency of the Parrot-jaw Defect. Two parrot-jaw heifers were detected among 650 females on the eight farms visited to measure normal Guernsey animals. Considering this as a random sample of the Guernsey breed, 3 in 1,000 or 0.3% of the Guernsey cattle have the defect.

Jersey. Three parrot-jaw cows were observed in the Kansas State University Jersey herd, all sired by a normal bull. This bull, Sparkle, also sired twenty-seven normal daughters in the herd. However, only 24 of his daughters, including the three parrot-jaws, reached 18-24 months of age. Only these were considered since the defect is not always expressed until

an animal reaches this age. The dams of the Sparkle daughters were sired by 10 different bulls. One bull was related to Sparkle, both having the same paternal grandsire. The nine other bulls were not related to Sparkle, but were related to each other in a slight degree.

The relationship of the three affected Jersey cows can be seen in figure 2.

Figure 2. Common ancestry of three parrot-jaw cows in the Kansas State University Jersey herd.



Since the defect is rare, the genes responsible for the defect would most likely be copies of those possessed by some single ancestor common to any two of the parrot-jaws, or to all three parrot-jaws. Since the only ancestor other than the sire common to 306C and 311C, was X, 306C probably received the copy through the maternal granddam rather than the maternal grandsire, as was most likely the case for 311C and 308C. Hence, the maternal grandsire

of 306C does not furnish any critical evidence relative to the inheritance of the defect.

Also, sire B was not related to Sparkle or sire A. Since the genes came from two lines, the frequency of the gene causing the defect might be greater than would ordinarily be expected from a single mutation.

Assuming a simple recessive gene hypothesis, all three bulls, Sparkle, A, and B, would be heterozygous. Sires A and B had been used in the herd prior to Sparkle. Table 1 shows the matings of these heterozygous bulls with each other's daughters.

Several other experimental matings also were made in the Kansas State University Dairy Genetics project herd. Sparkle was mated to two parrot-jaw Jersey cows. Both calves were normal. He also was mated to two of his daughters, to a normal crossbred Guernsey-Jersey, and to an affected Guernsey-Jersey crossbred. Again all calves were normal.

Still other matings were made with a parrot-jaw Jersey bull, Y. He sired four normal calves; two from an inbred Sparkle daughter and one each from two normal daughters of a parrot-jaw cow. The genealogy showing all experimental matings with Jerseys is on Plate I.

The results of all of these matings are shown in table 1. The hypothesis that the character is inherited as a simple recessive in the Jersey breed was tested.

The probability is such that the hypothesis of a simple recessive inheritance cannot be discarded. However, the bull calves were not raised, so it is not known if any of them would have expressed the defect later in life. Based on the information in the Kansas State University Jersey herd and in the experimental Jersey herd, there is no reason to reject the original hypothesis that in Jerseys the defect is inherited as an autosomal recessive character.

EXPLANATION OF PLATE I

I	1. G-6	II	1. 35A	III	1. 73A	IV	1. 071B	V	1. 022C
	2. 28A		2. 6B		2. 9B		2. 46B		2. 072B
	3. 29A		3. 5B		3. 45B		3. 0360C		
	4. Sparkle		4. 309C		4. Y		4. 0388C		
			5. J-12		5. 364C				
			6. J-3		6. 337C				

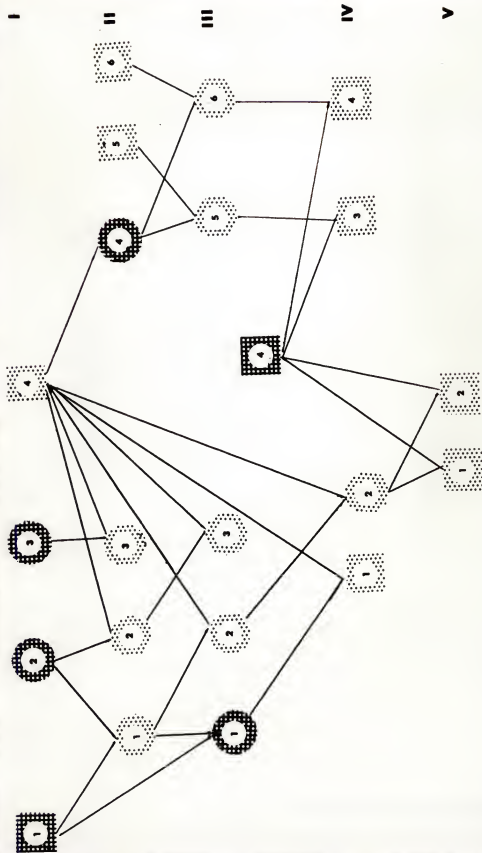


PLATE I

Genealogy of parrot-jaw matings in the Kansas State University Dairy Genetics Project Herd.

Table I. Tests of simple recessive hypothesis based on the matings in the Jersey breed.

Genotype	No.	Offspring		Observed		χ^2
		Expected Normal	Expected Affected	Normal	Affected	
Bb x bb	1	2	2	4	0	4.000
Sparkle x 28 & 29	2					
Y x 337 & 364	2					
Bb x Bb	7	5.25	1.75	5	2	.0481
Sparkle x Dau. of A	1					
Sparkle x Daus. of B	3					
B x Dau. of B	1					
Sparkle x 35A & 6B	2					
bb x B	2	1.40	0.60	2	0	.8570
Y x 46B	2					
Bb x B	1	0.85	0.15	1	0	.1760
Sparkle x 73A	1					
						5.081
d.f. = 3, 0.25 > P > 0.10						

Guernsey-Jersey Crosses and Backcrossing of Descendants to Affected Guernsey Bulls. Matings were made between the original parrot-jaw Guernsey bull, G-6, and three parrot-jaw Jersey cows (28A, 29A, and 53A). The resulting calves were all normal. These results prompted further Guernsey-Jersey crosses and backcrossing of the offspring to G-6, his affected son 0458B, and his affected double grandson 0490B. The genealogy of these crosses and backcrosses is on plate II. The matings in this herd are summarized in table 2.

As can be seen from the table all nine first generation crossbreds were normal. When 3 of these crossbreds were backcrossed to parrot-jaw Guernsey bulls, 3 of seven calves had the defect. This ratio was tested against the

EXPLANATION OF PLATE II

<p>I 1. G-6 2. 53A 3. 29A 4. 28A 5. Sparkle</p>	<p>II 1. 0458B 2. 074A 3. 33B 4. 054A 5. 37A 6. 55A 7. 76A 8. 5B 9. 055A 10. 50A 11. 35A 12. 6B</p>	<p>III 1. 0490B 2. 65B 3. 84B 4. 34B 5. 55B 6. 43B 7. 96B 8. 12C 9. 85A 10. 73A 11. 9B 12. 078A 13. 037A 14. 45B</p>	<p>IV 1. 017B 2. 64B 3. 092A 4. 073A 5. Ab 6. 089A 7. 071A 8. 46B</p>	<p>V 1. Z 2. 097A</p>
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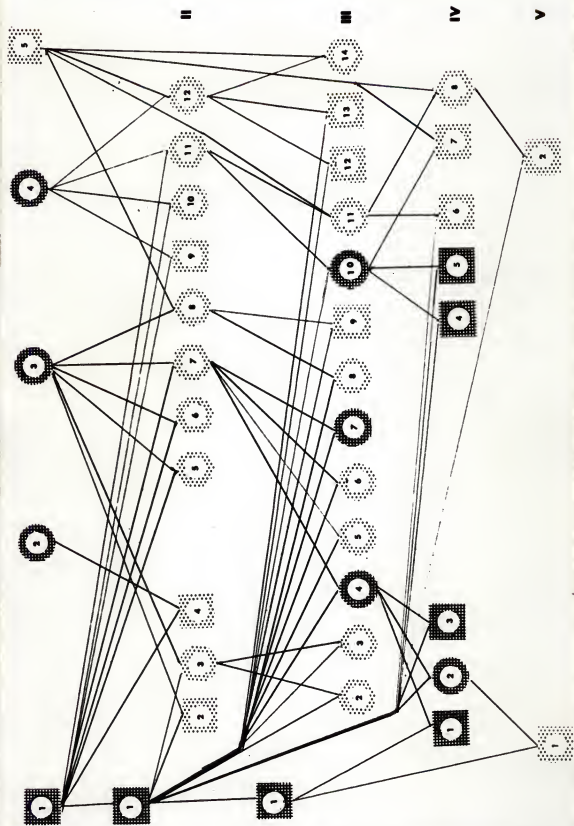


PLATE II

Genealogy of parrot-jaw Guernsey-Jersey matings and backcrosses to parrot-jaw Guernseys.

Table 2. Results of mating parrot-jaw Guernsey bulls both with parrot-jaw Jersey cows, and with the resulting crossbred offspring.

Mating Type	Offspring	
	Affected	Normal
Affected Guernsey x Affected Jersey	0	9
G-6 x 28A, 29A, & 53A	0	7
0458B x 29A	0	2
Affected Guernsey x Normal (F_1 crossbred)	3	4
G-6 x 35A	1	0
0458B x 76A & 33B	2	4
Affected Guernsey x Affected crossbreds (2nd generation)	5	0
0458B x 73A & 34B	4	0
0490B x 34B	1	0
Affected Guernsey x Affected crossbred (3rd generation)	0	1
0490B x 64B	0	1

hypothesis of simple recessive inheritance. The probability was such that the hypothesis was accepted ($P = 0.73$, d.f. = 1). The backcrossing of these parrot-jaw crossbreds to Guernsey bulls gave five third-generation cross-breds. All these animals were parrot-jaws. This true breeding of the recessives further supported a simple recessive mode of inheritance. However, one of the third generation parrot-jaw females (64B) calved very recently to the service of a parrot-jaw Guernsey bull (0490B) and the calf was normal. This refuted the hypothesis of a single recessive gene as the only factor governing the inheritance of the condition in the crossbreds.

Because all nine calves from the first crosses of Guernsey on Jersey were normal, different genes must be responsible for the condition in these two breeds. If the same genes with the same action controlled the character in both breeds, first generation crossbreds should show the defect. Figure 3

shows what would be expected with the same and with different genes acting in these crosses.

Figure 3. Illustration of gene action controlling parrot-jaw in Guernsey, Jersey, and Guernsey-Jersey crosses.

If genes acting were the same:		If genes acting were different:	
Guernsey sire	Jersey dam	Guernsey sire	Jersey dam
Genotypes: aa	aa	AAbb	aaBB
Phenotypes: (parrot-jaw)	(parrot-jaw)	(parrot-jaw)	(parrot-jaw)
F ₁		F ₁	
Genotypes: aa		AaBb	
(parrot-jaw)		(normal)	

Guernsey. In the genealogy of the experimental Guernseys (see page 24), normal offspring were obtained from the mating of affected parents and affected offspring were obtained from the mating of two normal animals. These results eliminated the possibility of a single gene, dominant or recessive, type of inheritance as the sole factor controlling the defect.

With these two inheritance schemes eliminated, one must consider a more complex type of inheritance. Two independent genes and incomplete penetrance hypotheses were considered. Of the nine independent two-gene types of inheritance listed by Snyder (11), all, except duplicate recessive epistasis and dominant and recessive epistasis, can readily be excluded. These can be eliminated either because they have more than two phenotypes or because one of the phenotypic groups will breed true.

For duplicate recessive epistasis and dominant and recessive epistasis, the nine possible genotypes and the corresponding phenotypes are listed in table 3.

EXPLANATION OF PLATE III

I
1. G-6
2. 437B
3. 444B
4. G-18
5. 436B
6. G-17
7. VFJ

II
1. 458B
2. 443B
3. 445B
4. 450B
5. 0458B
6. 465B
7. G-19
8. 449B
9. 462B
10. 470B
11. 434B

III
1. 483B
2. 471B
3. 492B
4. 480B
5. 0490B
6. 477B
7. 0403B
8. 0496B
9. 484B
10. G-30
11. 0488B
12. 0494B
13. 493B
14. 481B
15. 0479B

IV
1. 0406C
2. 402C
3. 404C
4. 499B
5. 0412C
6. 0400C
7. 400C
8. 496B
9. 401C

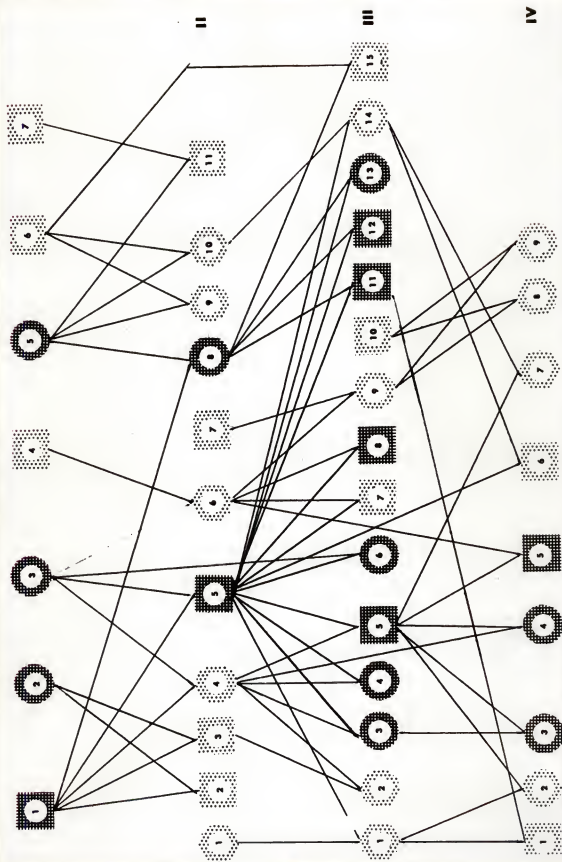


PLATE III

Genealogy of parrot-jaw Guernsey matings in the Kansas State University Dairy Genetics Project Herd.

Table 3. Genotypes and phenotypes under duplicate recessive epistasis and dominant and recessive epistasis.

Genotypes	Phenotypes	
	duplicate recessive	dominant and recessive
AABB	Normal	Normal
AABb	Normal	Normal
AaBB	Normal	Normal
AaBb	Normal	Normal
AAbb	Affected	Normal
Aabb	Affected	Normal
aaBB	Affected	Affected
aaBb	Affected	Affected
aabb	Affected	Normal

These genotypes were fitted to the mating results in the Guernsey breed and in the Guernsey-Jersey crosses. Fitting a two-gene hypothesis, in contrast to a one gene hypothesis, requires more attention be given to gene frequencies in the original breeding group, or groups, from which the foundation parrot-jaw animals came.

Chance events and subdivision and subsequent inbreeding within the breeding group permit wide fluctuation in the gene frequency when considering a single gene hypothesis. In the case of a two-gene hypothesis, however, one must account for two mutations occurring either simultaneously or at different times and becoming established at the frequencies required to fit the observed parrot-jaw in the breeding group.

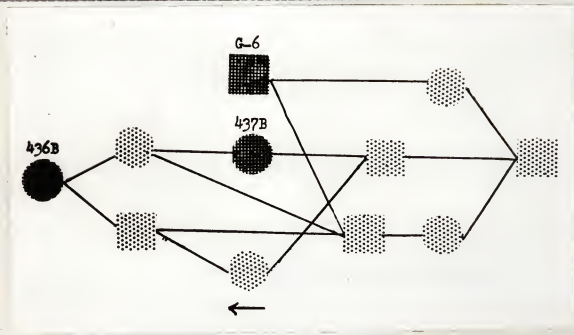
Since the frequencies of each of the two-gene genotypes are functions of the frequencies of those genes, certain of the genotypes will have a greater frequency, depending upon the difference in the relative frequencies of the two genes.

Therefore, one must consider not only how well the two-gene scheme fits the observed mating results, but how such a genetic situation, in relation to

the gene frequencies, could have come about in the breed and more particularly in that segment of the breed from which the foundation parrot-jaw animals were selected.

In the Guernsey herd, three of the four foundation animals were related with a mean coefficient of parentage of .148. Their relationship can be seen in figure 4.

Figure 4. Relationship of three foundation parrot-jaw Guernsey animals.



Since these animals were closely related, it would be likely that all received copies of the same mutant gene rather than copies of two different mutant genes. Hence, one would suspect that they would be homozygous at the same locus and thus produce all affected offspring. Such was not the case as can readily be seen from the genealogy. The two matings of the affected bull G-6, with cow no. 437B produced two normal calves.

To account for these results with duplicate recessive epistasis, G-6 and 437B would have to have been homozygous for recessive genes at different loci. Because of their close relationship, this would have occurred only if the

frequency of both recessive genes in the population was high. If, on the other hand, both genotypes $aaBB$ and $AAbb$ occur with equal frequency, the animals could be as closely related as they are and still have different genotypes although less likely than having the same genotypes. Therefore, while duplicate recessive epistasis is not likely to be the mode of inheritance, it cannot be excluded as a possible solution to the inheritance of the short-jaw condition in these Guernseys.

Another mode of inheritance which was considered was dominant and recessive epistasis. In this inheritance scheme, A is epistatic to B & b , and bb is epistatic to A & a . Affected animals would be of two genotypes ($aaBB$ and $aaBb$). The $aaBB$ animals would breed true, but matings of two $aaBb$ animals would produce 1 normal to 3 affected offspring. The normal animal would be the result of bb being epistatic to aa . With this mode of inheritance, the related foundation animals could be heterozygous for the B gene and thus be capable of producing both normal and abnormal calves. This type of inheritance also fits all other matings that were made since the founding of the Guernsey herd.

When the genes causing parrot-jaw in the Guernsey breed were crossed into the Jersey breed, the character behaved as a single recessive for three generations. It also seems likely that only a few other loci, possibly only one, are involved because only three successive backcrosses were required to produce a normal calf. Furthermore, because the defect does not breed true, dominance must be involved within one of these other loci.

These other genes would, of course, have been crossed into the Jersey breed along with the major recessive gene. Furthermore, the frequency of these secondary genes could have been quite different in the Jersey breed than in Guernseys. Because the major gene appeared as a simple recessive for three

generations, the dominant secondary allele at the second locus, or alleles at additional loci, may have been homozygous in these foundation Jerseys. The results in the crossbred herd can be interpreted to support either the duplicate recessive enistasis or the dominant and recessive enistasis hypothesis.

On one hand, if one assumes that these foundation Jerseys were homozygous for these other genes, or gene, the transfer of the character into the Jersey breed would have appeared as a recessive under the dominant and recessive epistasis hypothesis. This would happen because there would have been no recessive b genes to be enistatic to the recessive a gene, except those that may have been transferred from the Guernseys. Therefore, the recessive a gene could express itself all of the time in the presence of dominant B genes.

On the other hand, if one considers the case of duplicate recessive epistasis, the results in crossbreds can be interpreted to support this postulate. All matings in the crossbred herd were to three bulls. Since these bulls are a sire, G-6, his son O458B, and grandson O490B, it is reasonable to suspect that they were of the same genotype for the parrot-jaw defect. Therefore, only one genotype was introduced into the Jersey breed. As long as all animals have the same genotypic make-up they will breed true.

The Outstanding Excention. The recent birth of a normal calf from a parrot-jaw Guernsey, O490B, and a parrot-jaw crossbred heifer, 64B, is the only case where the defect did not breed true in the crossbreds. This normal calf can be explained with either duplicate recessive epistasis or dominant and recessive enistasis.

Under the duplicate recessive enistasis hypothesis, the son of the foundation bull would have been heterozygous. The presumed genotypes of the bulls used in this herd can be seen in figure 5.

With these possible genotypes, O458B would be equally likely to introduce

the gene into the Jerseys as he would the A. gene. The dam (64B) of the normal calf Z was an inbred daughter of 0458B. Hence, she has a .375 probability of carrying the a gene and a .625 probability of carrying the A gene. Because she is parrot-jawed, she would have to be recessive for the b gene under this hypothesis. The sire of the calf, 0490B, has .6 probability of A, .6 probability of a, .1 probability of B and .9 probability of b. The possible genotypes of the calf are shown in table 4.

Figure 5. Presumed genotypes of Guernsey bulls used in the experimental herd assuming duplicate recessive epistasis.

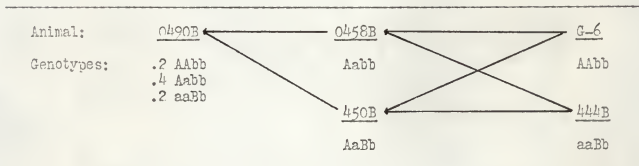


Table 4. Possible genotypes and their frequency which would occur from the mating of 64B and 0490B assuming duplicate recessive epistasis.

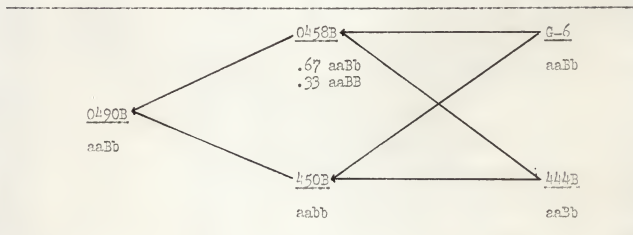
Gametes from 64B	<u>Gametes from 0490B</u>			
	.04 AB	.36 Ab	.06aB	.54 ab
.375 ab	<u>.0150 AaBb</u>	.1350 Aabb	.0225 aaBb	.2025 aabb
.625 Ab	.0250 AABb	.2250 AAbb	<u>.0375 AaBb</u>	.3375 Aabb

The only genotype in his array that would yield a normal calf is AaBb. Summing the probabilities associated with the two ways that this genotype could occur, a figure of .0525 is obtained. Thus, under this hypothesis, the birth of a normal calf is possible, although very improbable. These results

throw some doubt on duplicate recessive epistasis being the mode of inheritance of parrot-jaw in Guernseys.

Under the dominant and recessive epistasis hypothesis where the foundation animals were heterozygotes, the bulls again could transfer either allele of the recessive epistatic gene into the Jersey breed along with the major recessive gene. The presumed genotypes of the bulls for this hypothesis are in figure 6.

Figure 6. Presumed genotypes of Guernsey bulls used in the experimental herd assuming dominant and recessive epistasis.



Under this hypothesis, the dam, 64B, of the normal calf (Z) has a .77 probability of having B, a .23 probability of having b, and must have aa to be parrot-jawed. The sire, 0490B, has .5 probability associated with both B and b. The mating of these two animals and the possible genotypes of their offspring are shown in table 5.

The only genotype that would produce a normal calf is aabb. The probability associated with this genotype is .115. Under this hypothesis the probability of a normal calf being born to this mating is over twice the probability assuming duplicate recessive epistasis. Based on the chances of getting a normal calf from this mating, dominant and recessive epistasis

Table 5. Possible phenotypes and their frequency which would occur from the mating of 64B and 0490B assuming dominant and recessive epistasis.

Gametes from 64B	Gametes from 0490B	
	.5 aB	.5 ab
.77 aB	.385 aaBB	.385 aaBb
.23 ab	.115 aaBb	<u>.115 aabb</u>

is more likely to be the mode of inheritance of the defect in Guernseys than is duplicate recessive epistasis.

Another alternative hypothesis is an incompletely penetrant recessive gene. This has not been thoroughly tested. Parrot-jaw calves have resulted in twelve out of fifteen matings of two parrot-jaw animals. In one other case, the mating of the normal offspring of affected parents has produced a normal calf. If the character were single gene recessive, one would expect all of these matings to produce affected calves. However, only the twelve were parrot-jawed. This gives a penetrance of 75%. At the present time, there is not enough information available to suggest what might be the cause of the 25% being normal. Some other possibilities might be multiple gene action, a threshold effect, or some other combination of dominance and epistasis.

Guernsey-Holstein Crosses. Two mating of a Guernsey bull (0458B) and a parrot-jaw Holstein cow produced two normal calves. Since both calves died shortly after birth, it is not known whether the defect might have shown up in later life as it does in the Jersey breed.

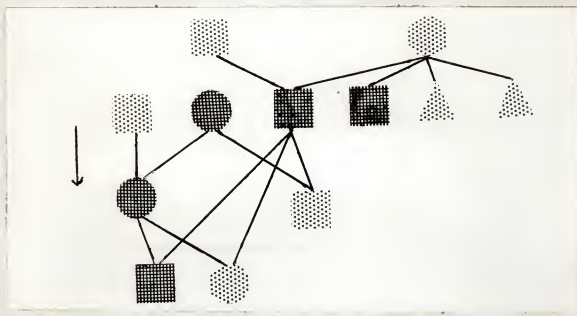
These results, as in the Guernsey-Jersey matings, indicate different genes may be involved in these two breeds.

Brown Swiss. Matings in the Brown Swiss breed are shown in table 6. The genealogy is in figure 7.

Table 6. Experimental parrot-jaw matings in the Brown Swiss breed.

Sire	Dam	Offspring	
		Normal	Parrot-jaw
Parrot-jaw	x Parrot-jaw	2	1
Normal	x Parrot-jaw	0	1

Figure 7. Genealogy of parrot-jaw Brown Swiss matings.



These matings indicate a mode of inheritance similar to that in Gaernseys. The parrot-jaw bull used in these matings had a maternal brother that was also parrot-jawed. Since the dam of these two was normal, the condition would have to be inherited as a recessive unless two dominant mutations has occurred simultaneously. The probability of this happening is so small as to eliminate it from serious consideration.

The mating of two parrot-jaw animals produced both normal and parrot-jaw

offspring, thus seemingly eliminating single recessive gene inheritance. The normal female from this mating was observed to be normal at maturity but the bull calf was not raised. Since so few matings were made within this breed, and no crossbreds were born, no specific mode of inheritance is postulated. However, a single gene dominant or recessive inheritance can be eliminated from the possible modes of inheritance if, indeed, all affected animals do exhibit the characteristic at birth.

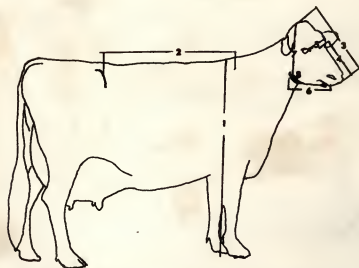
Morphology and Anatomy

Measurements were taken on parrot-jaw head in attempting to establish which parts of the head are affected in the expression of the defect. It was also thought that knowing which bone or bones are affected would give some clue as to the complexity of the inheritance. The dimensions of parrot-jaw heads were compared with normals. These comparisons were made on live animals and on the heads of the animals after they had left the herd.

All of the measurements considered in this study were taken on female Guernsey animals. Some bull heads and all of the crossbred heads, along with calves' heads were kept, but there were so few animals in any one age group that no comparisons were made. The measurements on macerated heads includes only cows over 3 years of age. This was done because there was no other age group which contained more than 1 parrot-jaw or 2 control heads. It was also learned from the measurement of live animals that after 3 years of age there is very little growth in the bones of the head, making it possible to group all animals over 3 years of age in one class and thus gain numbers within one class.

Measurement of Live Animals. The measurements that were taken on the live animals are shown in figure 8.

Figure 8. Measurements taken on both normal and parrot-jaw Guernsey females.



- 1) height at the withers
- 2) length along the top of the back from the anterior edge of the scapula to the hooks
- 3) head length from poll to muzzle
- 4) nose length from point between the eyes to the muzzle
- 5) distance between the eyes at the edge of the supraorbital ridge
- 6) mandible length from the angle to the anterior extremity
- 7) length from the poll to the angle of the mandible
- 8) width of the mandible at the angle

The animals measured were divided into 10 separate groups according to age. The groups were; 0-91, 92-182, 183-273, 274-365, 366-456, 457-547, 548-730, 731-1095, 1096-1460, and over 1460 days of age. Appendix table 1 shows the means, standard deviations, and coefficients of variation for each group and measurement. The values obtained for height at the withers corresponds closely to the tables for Guernsey females listed by Brody (?). For each measurement, the value was regressed upon the age of the animal and the value of b computed. These values are in appendix table 2. These values indicate that growth is quite rapid for the first six months. After this time the rate of growth is somewhat slower and continues at this slow rate until

two-three years. After this age there is very little increase in skeletal growth. These results also correspond closely with the tables listed by Brody (2). These tables show very little change in skeletal measurements after three years of age.

While measuring these females, two parrot-jaw calves were discovered. They were measured, but not included in calculating the data.

Using the equation $\hat{Y} = \bar{y} + b (X - \bar{x})$ where \hat{Y} = the predicted value of the measurement, \bar{y} = the mean value of the measurements in that group, b = the slope of the regression line, X = the age of the calf in days, and \bar{x} = the mean age for the group, estimates were made of the measurement values on these two calves. These estimates were subtracted from the actual measurement to find the deviation from the prediction.

There were four parrot-jaw females in the experimental herd. These were measured in the same manner at different stages of development. Three of these were measured three times each and one was measured twice. The values of the measurements for these heifers was predicted in the same manner as the field cases. The deviations from this predicted value were noted. The deviations for both the field cases and the experimental animals are in appendix table 3. Appendix table 4 shows these deviations expressed in terms of standard deviations. The deviations of all of the estimates were summed and the average taken. The results are listed in table 7, showing the mean deviations of the 11 experimental herd measurements in the first column and the total including the two field cases in the second.

Individually, none of the deviations are statistically significant. The greatest differences are in the width of the head. Both the width at the eyes and the width of the mandible are nearly one standard deviation less in the parrot-jaw animals when compared to the value predicted from normals in

the combined group. The values also indicate a shorter mandible and a longer upper jaw. One other measurement that has a large deviation is the poll to the angle of the mandible. This measurement indicates that the parrot-jaw animals are somewhat shallower in the head.

Table 7. Differences between parrot-jaw and normal females for the 8 measurements in Figure 8 (deviation from the predicted value for appropriate age, expressed in terms of the standard deviation).

Measurement	11 Experimentals	11 Experimentals +2 field cases
Height at withers	.329	.219
Back measurement	.628	.500
Head length	.454	.441
Nose length	-.499	-.303
Width at eyes	-1.180	-.983
Mandible length	-.205	-.620
Poll to angle of mandible	-.780	-.687
Mandible width	-1.035	-.911

Measurement of Butcher-skinned Heads. The values for the dimensions obtained on the butcher-skinned heads are listed in appendix tables 5 and 6. Comparing the means of the two groups, it is apparent that the parrot-jaw animals had larger heads as all measurements were larger in this group. Therefore, all of the measurements were divided by the length of the head. This puts both groups on a percentage basis and these figures are compared. Table 8 shows the differences between the two groups, both on an actual measurement basis and on a percentage basis.

The comparisons of these means on a percentage basis is listed in table 9 along with a description of each difference.

Table 8. Comparison of the means of 12 different measurements on 4 parrot-jaw and 9 control heads (butcher-skinned).

Measurement	Actual value			Measurement head length		
	Parrot-jaw	Normal	Difference (PJ-N)	Parrot-jaw	Normal	Difference (PJ-N)
1	18.03cm	17.06cm	0.97cm	.357	.368	-.011
2	20.18	18.37	1.81	.400	.396	.004
3	1.50	1.13	.46	.003	.002	.001
4	30.53	28.16	2.42	.606	.607	-.001
5	50.50	46.38	4.12	1.000	1.000	—
6	30.63	29.69	.94	.607	.640	-.033
7	48.65	47.50	1.15	.963	1.024	-.061
8	70.58	69.73	.85	1.398	1.481	-.083
9	43.55	39.39	4.16	.862	.849	.013
10	31.93	30.58	1.35	.632	.659	-.027
11	15.50	13.82	1.68	.307	.293	.009
12	26.13	24.57	1.56	.517	.530	-.013

Table 9. Description of relative differences between parrot-jaw and normal animals (butcher-skinned).

Mens. No.	Difference (PJ-N)	Description
1	-.011	shorter on transverse plane at level of union of nasals and frontals to edge of orbital ridge
2	.004	longer from poll to union of nasals and frontals
3	.001	deeper dish
4	-.001	shorter from fronto-nasal junction to premaxillae
5	—	head length
6	-.033	poll to angle of mandible
7	-.061	less in circumference of head at 1st cheek tooth
8	-.083	less in circumference of head at last cheek tooth
9	.013	longer from angle of mandible to premaxillae
10	-.027	less in circumference of jaws posterior to dental pad
11	.009	wider at the angle of the mandible
12	-.013	shorter from the angle of the mandible to the supra-orbital ridge

The most striking differences are in the denth and circumference values.

These indicate that the parrot-jaw animals are shallower in the head than are the normals. This can also be shown by dividing the distance from the poll to the angle of the mandible by the length of the skull and by the length of the mandible. When dividing by the length of the skull, figures of 70.18 and 75.16 are obtained for the parrot-jaw and control groups respectively. Dividing by the length of the mandible, figures of 60.59 are obtained for the short-jaw and 63.81 for the normal group. These figures also indicate that the head is deeper in the control group in comparison to either the length of the mandible or the length of the skull.

Macerated Heads. After maceration, measurements were taken on the mandible and skull bones. The measurements taken are shown in appendix plates I and II and the values of the measurements are in appendix tables 7, 8, 9, and 10. Again the values obtained for the skull are divided by the skull length and the mandible values divided by the mandible length since the parrot-jaw animals are larger. These values are in appendix tables 11, 12, 13 and 14. The two groups are compared on an actual and percentage basis in table 10.

The differences in the two group means on the percentage basis are listed in table 11 along with a description of each difference.

The comparison indicates that the distance from the molar teeth forward is somewhat shorter in the parrot-jaw group. The molar space is the same on the percentage basis in both groups. This is similar to the results of Nordby, et al (3) who found that all portions of mandible of overshot ewes were shorter than normal but that the molar space was only slightly shorter and that the greatest shortness was in the anterior parts of the mandible. These figures also suggest that the maxilla of parrot-jaw animals is longer. Similar results were obtained by Gruneberg and Lea (4) and by Nordby et al (8).

Two other measurements that show considerable difference are the depth and

width of the head. The width as measured at the zygomatic arch of the skull is quite a bit narrower in the parrot-jaw group than in the controls. Likewise the width at the angle of the mandible is narrow in the short-jaw heads. The depth of the head as measured both from the coronoid process to the base of the mandible and the distance from the poll to the base of the skull show the parrot-jaw group to be shallower.

Table 10. Comparison of the means of 25 different measurements on 4 parrot-jaw and 9 control heads (macerated).

<u>Actual</u>			<u>Percentage</u>		
<u>Parrot-jaw</u>	<u>Normal</u>	<u>Difference</u> (PJ-N)	<u>Parrot-jaw</u>	<u>Normal</u>	<u>Difference</u> (PJ-N)
MANDIBLE					
1	38.4cm	36.2cm			
2	11.4	11.2	.297	.309	-.012
3	12.7	12.8	.331	.354	-.023
4	7.1	6.1	.185	.169	.016
5L	11.9	10.4	.310	.287	.023
W	2.1	1.8	.055	.050	.005
6L	6.6	7.4	.172	.204	-.032
W	2.1	1.8	.055	.050	.005
7	36.0	35.0	.951	.967	-.016
8	22.1	21.9	.576	.605	-.029
9A	18.1	17.5	.471	.483	-.012
B	24.8	23.7	.646	.655	-.009
10A	38.8	35.7	1.010	.986	.024
B	28.7	26.5	.747	.732	.015
C	11.4	11.2	.297	.309	-.012
SKULL					
1	51.3cm	44.9cm			
2	50.0	44.1	.975	.982	-.007
3	10.6	9.8	.207	.218	-.011
4	19.4	21.0	.378	.468	-.090
5	10.3	8.1	.201	.180	.021
6	5.7	5.1	.111	.114	-.003
7	11.9	7.3	.232	.207	.025
8	4.3	3.7	.084	.082	.002
9	19.2	18.8	.374	.419	-.045
10	27.3	23.1	.532	.514	.018

Table 11. Description of relative differences between parrot-jaw and normal heads (macerated).

Difference (PJ-N)		MANDIBLE
		The parrot-jaw heads are:
2	-.012	shorter from first cheek tooth to 4th incisor
3	-.023	shorter from first cheek tooth to 1st incisor
4	.016	longer from mental foramen to anterior
5	.023	longer from cheek tooth to L of mandible
5b	.005	wider at cheek tooth
6	-.032	shorter from cheek tooth to base
7	-.016	shorter from posterior base to anterior
8	-.029	shorter from coronoid process to base
9	-.021	shorter from mental foramen to anterior base
B	-.009	shorter from anterior base to extremity
10	.024	longer from mandibular condyle to 4th incisor
B	.015	longer from mandibular condyle to 1st cheek tooth

SKULL

2	-.007	shorter from premaxilla to nuchal eminence
3	-.011	shorter from occipital condyle to nuchal eminence
4	-.090	shorter from highest point to base of skull
5	.021	longer from cheek tooth to anterior border of maxilla
6	-.003	shorter from anterior maxilla to anterior premaxilla
7	.025	longer along junction of maxilla and premaxilla
8	.002	longer lacrimal
9	-.045	narrower at zygomatic arch
10	.018	longer maxilla from anterior to sylvoid process

Wordby et al (8), found that the ratio of mandible length to skull length reflects the severity of the defect more clearly than any single measurement. This same ratio is shown by M_1/S_1 . All of the normal group are over 77%, while all short-jaws are less than 77%. The normal cow 422 had an extremely long, narrow head and thus gave a ratio that was considerable lower than the rest of the normal group.

SUMMARY

This study was conducted to determine the inheritance of brachygnathia in

dairy cattle and to describe any morphological or anatomical differences that existed in the expression of the defect.

The parrot-jaw defect was observed in 34 animals in four dairy breeds: Jersey, Guernsey, Holstein, and Brown Swiss. The incisors of affected animals meet $\frac{1}{4}$ - $1\frac{1}{2}$ inches posterior to the dental papilla, most commonly between the first and second dental ridges. The defect is a slight handicap to eating but has no other apparent effects.

Evidence concerning the inheritance of the defect was obtained from several sources. The condition was observed in three females in the Kansas State University Jersey herd and in two females and one bull in the Garden City Branch Station Brown Swiss herd. Experimental matings for four generations in the Jersey and Guernsey breeds and three generations of repeated backcrossing Jersey cows and their descendents to Guernsey bulls were made in the Kansas State University Dairy Genetics Project herd. These experimental matings have involved more than eighty animals.

Some study of the morphology of the defect was done on heads of animals in the experimental herd and the University Jersey and Guernsey herds. Still other information came from the measuring of 255 normal Guernsey females in eight Kansas herds.

In these herds two parrot-jaw heifers were observed. Thus, the frequency of occurrence of the defect in the Guernsey breed was estimated at 3 in 1,000.

The parrot-jaw defect in Jerseys appeared to be different morphologically from that in the other breeds. Experimental matings indicated that the inheritance of parrot-jaw in Jerseys was also different. Evidence obtained, both from experimental matings and from the Kansas State University Jersey herd, did not refute a simple recessive mode of inheritance of parrot-jaw in this breed.

Not only did parrot-jaw in the Guernsey breed appear to be a morphologically different type from that in Jerseys, but it differed also in that it was always expressed at birth. The inheritance of the defect in this breed seemed to be more complex. Neither a dominant nor a recessive mode of inheritance satisfactorily explained all mating results. Of the two suitable epistatic gene schemes considered — dominant and recessive epistasis and duplicate recessive epistasis — the former fitted not only the pedigree information of the three related foundation animals better than did the latter, but it also better fitted the results of experimental matings.

In repeated backcrossing of Jersey cows and their descendants to parrot-jaw Guernsey bulls, dominant and recessive epistasis explained the occurrence of a normal calf from affected parents more satisfactorily than did duplicate recessive epistasis.

The results of Brown Swiss matings, like those in Guernseys, indicated a complex mode of inheritance. Although no definite mode of inheritance can be stated, single gene dominant, or recessive, inheritance can be eliminated.

Since all first generation Guernsey-Jersey and Guernsey-Holstein cross-bred animals were normal, the defect seemed to be controlled by different genes in these breeds.

In addition to the study of the inheritance, attempts were made to describe in detail the morphology of the defect in Guernseys. Numerous measurements were taken on parrot-jaw and normal heads, while intact, after butcher-skinning, and after maceration. Comparison of parrot-jaw and normal groups did not show a significant difference between groups for any measurement. However, six living parrot-jaw animals had narrower and shallower heads than did normals of comparable age. The upper jaws were longer and the mandibles, shorter.

The comparison of butcher-skinned heads indicated that parrot-jaw heads were shallower. The distance from the poll to the angle of the mandible was shorter in parrot-jaws than in the controls, as were various measurements of jaw circumference.

The results from comparing macerated heads of parrot-jaw and normal animals were very similar to those obtained by other procedures. Macerated parrot-jaw heads were narrower and shallower than normal control heads. The maxillae and premaxillae were longer than in normal animals.

All these results indicate that the defect in Guernseys may be the result of changes in both upper and lower jaws.

ACKNOWLEDGEMENTS

The author would like to thank all persons who helped in the collection of information that was used in this study. He also wishes to thank Dr. C. L. Norton, Head of the Department of Dairy Science, for his corrections and criticisms of this paper. Special thanks is expressed to Dr. Keith Huston. Without his guidance and assistance this study would not have been possible.

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APPENDIX

Table 2. Relative growth rate of live Guernsey females for each di-

	N =	0-91 27	92-182 27	183-273 24	274-365 18
Wither height		.148	.132	.028	.096
Back measurement		.130	.014	.028	.017
Head length		.062	.004	.023	.031
Nose length		.048	.044	.021	.055
Eye width		.032	.020	.016	.006
Length of mandible		.046	.036	.024	.019
Poll to angle of mandible		.041	.052	.019	.019
Width of mandible		.024	.019	.010	.003

mension as expressed by the regression of the measurement on age.

366-456 18	457-547 12	548-730 22	731-1095 24	1096-1460 27	1461 - 36
<hr/>					
.096	.031	.014	-.0030	-.0060	-.0001
.083	.013	.004	.0002	.0090	-.0040
.016	.002	.006	.0020	-.0020	.0002
.055	.028	.001	.0030	-.0020	.0010
.022	.009	-.003	.0004	-.0001	.0002
.009	.015	.010	.0030	-.0020	-.0001
.032	.014	.002	-.0020	-.0010	.0002
.007	.004	.001	-.0001	-.0010	.0003

Table 3. Actual differences between parrot-jaw and normal females for the 8

	64			493		
	568	658	792	391	482	615
Wither	3.53	1.59	.39	3.05	5.70	3.69
Back	4.19	3.81	4.19	4.02	5.31	4.97
Head	1.98	.79	.41	-.21	.45	1.35
Nose	1.48	-1.80	-2.79	1.53	-.81	-1.09
Eye Width	-.54	-1.12	-1.77	-1.00	-1.37	-.78
Mandible	-1.22	.71	.39	.29	-.03	1.34
Poll to angle	-1.19	-.78	-1.94	-1.26	-.89	-1.39
Width of mand.	-.43	.11	.09	.09	-.63	.27

measurements in figure 8 (expressed in centimeters).

492			499		Field A	Field B
LL0	531	664	39	129		
-4.68	3.18	3.50	-2.86	-3.00	-4.37	.89
.95	.67	8.77	-2.83	-1.56	-2.06	-.78
0.00	1.25	1.06	-.87	.60	.69	.40
-.67	-.98	-1.49	-.16	-1.61	.15	2.39
-.43	-1.71	-1.40	-.14	-2.04	1.87	-.96
-.65	-1.07	-1.05	-1.03	-.64	-2.34	-4.02
-1.13	-.38	-1.59	-.75	-1.36	-1.66	.61
-1.56	-2.83	-1.73	-1.77	-1.15	.81	-.95

Table 4. Actual differences between parrot-jaw and normal females for the 8

	64			493		
	568	658	792	391	482	615
Wither	.885	.396	.071	.663	1.428	.918
Back	1.174	.765	.927	.641	1.487	.998
Head	1.650	.467	.240	-.137	.375	.799
Nose	.612	-1.295	-1.603	.708	-.335	-.747
Eye Width	-.794	-1.436	-2.241	-.725	-2.015	-1.000
Mandible	-.782	.493	.215	.312	-.019	.931
Poll to angle	-.983	-.624	-1.128	-.558	-.736	-1.112
Width of mand.	-1.092	-.489	1.430	.070	-.716	.307

measurements in figure 8 (expressed as standard deviations).

L92			L99		Field A	Field B
440	591	664	39	129		
-1.017	.797	.871	-.659	-.587	-.950	.174
.152	.188	1.761	-.679	-.393	-.329	-.196
0.000	1.042	.627	-.506	.432	.451	.288
-.310	-.405	-1.021	-.092	-1.000	.451	.288
-.312	-2.514	-1.795	-.152	-2.582	1.355	-1.215
-.699	-.686	-.729	-.725	-.571	-2.516	-3.589
-.500	-.231	-1.272	-.581	-.850	-.735	.381
-1.209	-3.216	-1.965	-1.883	-1.322	.628	-1.092

Table 5. Actual measurement values obtained for the 12 different measurements on butcher-skinned normal heads (all in centimeters).

	456	494	445	459	460	422	430	469	464	\bar{x}
1	17.2	18.0	17.0	16.5	16.8	17.5	18.0	15.2	17.3	17.06
2	15.3	20.1	17.2	19.5	19.0	21.0	19.5	15.5	18.2	18.37
3	1.0	1.4	1.3	1.0	1.3	0.9	1.1	1.8	0.4	1.13
4	29.0	25.2	27.8	26.0	27.5	26.5	30.8	32.0	28.6	28.16
5	44.0	45.3	44.8	45.3	46.3	47.2	29.4	48.1	47.0	46.38
6	29.5	26.0	30.2	29.3	29.3	31.8	34.5	25.6	31.0	29.69
7	45.5	43.5	46.0	45.7	46.8	49.0	51.3	52.9	46.8	47.50
8	69.6	70.0	70.3	68.8	68.0	70.5	71.7	70.5	68.2	69.73
9	39.0	37.2	39.8	40.2	39.5	39.6	41.0	40.2	38.0	39.39
10	28.6	29.1	29.4	29.6	29.8	32.5	32.5	33.6	30.2	30.58
11	14.8	13.5	13.4	12.8	14.4	15.0	13.0	14.5	13.0	13.82
12	24.3	23.8	34.8	24.8	23.9	25.8	25.7	24.2	23.8	24.57

Table 6. Actual measurement values obtained for the 12 different measurements on parrot-jaw heads (all in centimeters).

	437	436	444	463	\bar{x}
1	16.5	20.0	17.6	18.0	18.3
2	18.2	20.0	21.0	21.5	20.18
3	1.75	1.0	1.6	2.0	1.59
4	31.8	31.0	33.0	26.5	30.58
5	49.5	51.0	54.0	47.5	50.5
6	30.5	31.0	33.0	28.0	30.63
7	46.0	48.0	50.0	50.6	48.65
8	70.0	69.0	69.2	74.1	70.58
9	43.2	45.0	43.5	42.5	43.55
10	32.2	31.0	31.5	33.0	31.93
11	17.5	14.0	16.0	14.5	15.50
12	25.4	26.0	27.5	25.6	26.13

EXPLANATION OF PLATE I

1. Anterior edge of premaxilla to most posterior margin of occipital condyle.
2. Anterior edge of premaxilla to most posterior margin of nuchal eminence.
3. Most posterior margin of occipital condyle to nuchal eminence.
4. When skull is set on a 4.5 cm block of wood, height from highest point of skull to base of skull.
5. Length from edge of first cheek tooth to anterior border of maxilla.
6. Length from anterior most junction of maxillae to anterior edge of premaxilla.
7. Length along junction of maxilla and premaxilla.
8. Lacrimal (dorsal angle of maxilla to anterior angle of frontal).
9. Width at zygomatic arch.
10. Length of maxilla from anterior angle to anterior edge of styloid process of the malar.

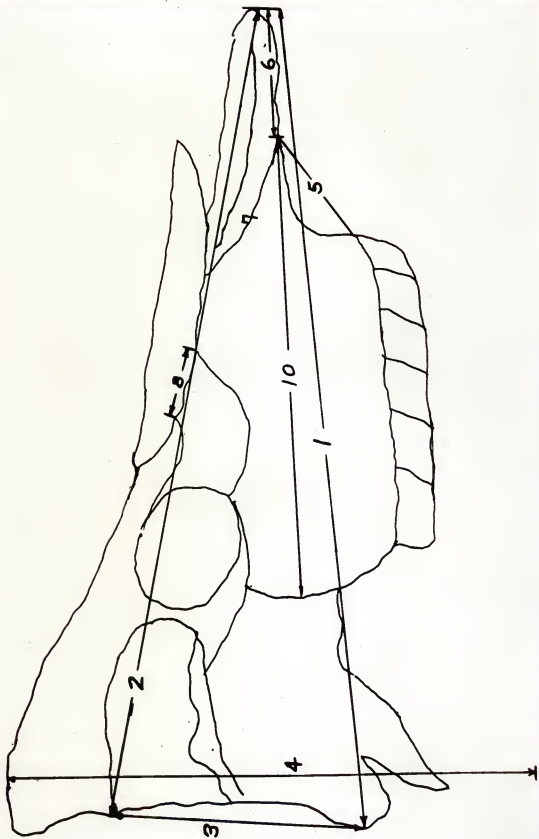


PLATE I

Measurements taken on both normal and parrot-jaw macerated skulls.

EXPLANATION OF PLATE II

1. Length (angle to anterior extremity).
2. Length from first cheek tooth to 4th incisor.
3. Length from first cheek tooth to 1st incisor.
4. Length from posterior part mental foramen to anterior extremity on plane parallel to dorsal border.
5. Length and width from last cheek tooth to angle of mandible.
6. Length and width from last cheek tooth to base of mandible.
7. Length from most posterior portion of base of angle of mandible to anterior extremity.
8. Height from coronoid process to base of mandible.
9. Slope of anterior edge of mandible.
 - A. Length from posterior part of mental foramen to anterior angle of base.
 - B. Length from anterior angle of base to extremity.
10.
 - A. Posterioormost angle of mandibular condyle to posterior edge of 4th incisor.
 - B. Posterioormost angle of mandibular condyle to anterior edge of 1st cheek tooth.
 - C. Anterior edge of first cheek tooth to posterior edge of 4th incisor.

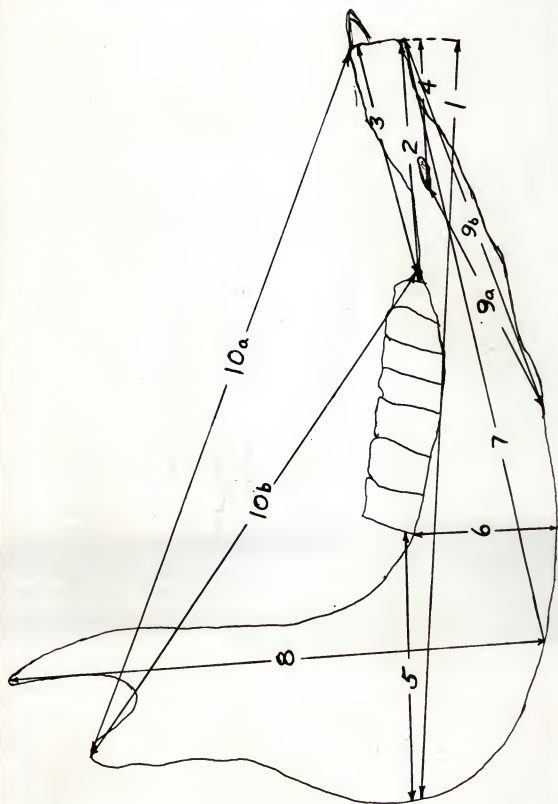


PLATE II

Measurements taken on both normal and parrot-jaw macerated mandibles.

Table 7. Actual measurement values obtained for the 15 different measurements on normal macerated mandibles (all values in centimeters).

	422	430B	469B	464B	456	494	445B	459	460
1	37.2	37.8	36.0	36.0	35.3	36.3	36.4	36.2	35.0
2	11.8	11.8	10.4	11.0	12.0	10.8	10.0	11.3	11.5
3	13.4	13.7	12.5	13.0	13.5	12.0	11.5	12.7	12.5
4	6.5	6.4	6.8	6.0	5.8	6.0	6.4	5.6	5.8
5L	11.4	12.0	10.7	9.6	9.2	10.0	10.8	10.5	9.5
W	1.9	1.7	1.9	1.7	1.5	2.0	1.8	2.0	1.8
6L	7.5	7.5	7.0	8.0	7.2	7.3	7.0	7.3	7.6
W	1.9	1.7	1.9	1.7	1.5	2.0	1.8	2.0	1.8
7	35.8	26.0	33.5	35.3	34.0	35.0	35.7	36.0	34.0
8	21.8	23.0	21.0	21.0	22.0	22.0	22.0	22.3	21.8
9A	17.5	19.5	16.2	18.1	18.5	17.8	16.5	17.1	16.5
B	24.0	25.7	22.5	24.2	24.4	23.6	23.0	23.3	22.5
10A	36.8	28.2	35.5	35.8	34.3	35.0	34.7	36.0	34.6
B	27.0	28.5	27.0	27.0	24.5	26.0	26.5	36.8	25.1
C	11.8	11.8	10.4	11.0	12.0	10.8	10.0	11.3	11.5

Table 8. Actual measurement values obtained for the 15 different measurements on parrot-jaw macerated mandibles (all values in centimeters).

	463	444	436	437B
1	39.0	38.2	38.9	37.3
2	11.0	11.6	11.0	11.8
3	12.5	12.8	12.3	13.0
4	7.0	7.0	7.0	7.2
5W	2.0	1.9	1.7	2.9
L	12.0	12.0	12.1	11.3
6W	2.0	1.9	1.7	2.9
L	7.0	6.8	6.0	6.7
7	27.2	36.8	36.8	35.0
8	22.5	22.3	22.2	21.4
9A	17.7	19.8	17.0	18.0
B	24.7	26.2	23.5	24.8
10A	38.4	37.8	38.0	41.0
B	29.0	28.3	28.2	29.2
C	11.0	11.6	11.0	11.8

Table 9. Actual measurement values obtained for the 10 different measurements on normal macerated skulls (all values in centimeters).

	422	430B	469B	464B	456	494	445B	459	460
1	47.8	47.6	45.5	45.2	52.5	42.5	44.2	44.5	43.6
2	47.0	47.2	44.9	46.0	41.0	43.0	42.5	43.4	41.5
3	11.0	10.4	9.7	10.4	8.5	9.8	9.0	9.6	9.5
4	22.0	21.9	21.5	18.7	17.7	25.7	21.0	19.8	21.0
5	9.2	9.0	7.2	7.5	8.0	7.9	8.0	8.6	7.7
6	5.8	4.3	5.8	5.8	5.0	4.6	4.6	4.4	5.4
7	10.6	9.7	7.5	9.5	11.5	9.8	7.8	8.5	8.7
8	4.0	3.6	3.5	4.1	4.0	3.5	4.0	3.6	3.0
9	19.0	19.8	17.9	18.3	18.1	18.5	19.0	19.4	19.0
10	24.3	24.5	22.7	23.6	21.5	22.8	23.0	23.5	22.0

Table 10. Actual measurement values obtained for the 10 different measurements on parrot-jaw macerated skulls (all values in centimeters).

	463	444	436	437B
1	51.5	52.7	51.0	50.0
2	49.5	51.0	49.8	49.5
3	11.0	10.5	10.0	11.0
4	22.5	18.8	18.5	17.6
5	10.5	10.6	10.3	9.8
6	5.4	6.3	5.4	5.6
7	11.2	11.2	10.0	15.1
8	3.9	4.7	5.0	3.5
9	19.0	19.5	20.5	17.6
10	27.5	28.0	27.3	26.5

Table 11. Standardized measurements on normal macerated Guernsey mandibles (obtained by dividing each measurement by the mandible length).

Mandible	\bar{x}	456	494	445	459	460	422	430	469	464	\bar{x}
1	36.2										
2	11.2	.340	.298	.275	.312	.329	.217	.312	.289	.306	.309
3	12.8	.382	.331	.316	.351	.357	.360	.362	.347	.361	.354
4	6.1	.164	.165	.176	.155	.166	.175	.169	.189	.167	.169
5L	10.4	.042	.055	.049	.055	.051	.051	.045	.053	.047	.287
W	1.8	.261	.275	.297	.290	.274	.306	.317	.297	.267	.050
6L	7.4	.042	.044	.049	.055	.051	.051	.045	.053	.047	.204
W	1.8	.204	.201	.192	.202	.217	.202	.198	.194	.222	.050
7	35.0	.963	.964	.981	.994	.971	.962	.952	.931	.981	.967
8	21.9	.623	.606	.604	.616	.623	.586	.608	.583	.583	.605
9A	17.5	.524	.490	.453	.472	.471	.470	.516	.450	.503	.483
B	23.7	.691	.650	.632	.644	.643	.645	.680	.625	.672	.655
10A	35.7	.972	.964	.953	.994	.989	.989	1.011	.986	.994	.986
B	26.5	.694	.716	.728	.740	.717	.726	.754	.750	.750	.732
C	11.2	.340	.298	.275	.312	.329	.317	.312	.289	.306	.309

Table 12. Standardized measurements on parrot-jaw macerated Guernsey mandibles (obtained by dividing each measurement by the mandible length).

Mandible	\bar{x}	437	436	444	463	\bar{x}
1	38.4					
2	11.4	.316	.283	.304	.282	.297
3	12.7	.349	.316	.335	.321	.331
4	7.1	.193	.180	.183	.179	.185
5L	11.9	.303	.311	.314	.308	.310
W	2.1	.078	.044	.050	.051	.055
6L	6.6	.180	.154	.178	.179	.172
W	2.1	.078	.044	.050	.051	.055
7	36.5	.938	.946	.963	.954	.951
8	22.1	.574	.571	.584	.577	.576
9A	18.1	.483	.437	.518	.454	.471
B	24.8	.665	.504	.686	.633	.646
10A	38.8	1.099	.977	.970	.985	1.010
B	28.7	.783	.725	.741	.744	.747
C	11.4	.316	.283	.304	.282	.297

Table 14. Standardized measurements on parrot-jaw macerated Guernsey skulls (obtained by dividing each measurement by the skull length).

Skull	\bar{x}	437	436	444	463	\bar{x}
1	51.3					
2	50.0	.990	.976	.968	.961	.975
3	10.6	.220	.196	.199	.214	.207
4	19.4	.352	.363	.357	.437	.378
5	10.3	.196	.202	.201	.204	.201
6	5.7	.112	.106	.120	.105	.111
7	11.9	.302	.196	.213	.217	.232
8	4.3	.070	.098	.089	.076	.084
9	19.2	.384	.402	.370	.369	.374
10	27.3	.530	.535	.531	.534	.532
M_1		.7460	.7627	.7248	.7572	.7485
$\frac{M_1}{S_1}$						

BRACHYGNATHIA IN DAIRY CATTLE

by

STANLEY THOMAS SMITH

B. S., Kansas State University, 1959

AN ABSTRACT

submitted in partial fulfillment of the
requirements for the degree

MASTER OF SCIENCE

Department of Dairy Science

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1963

This study was conducted to determine the inheritance of brachygnathia in dairy cattle and to describe any morphological or anatomical differences that existed in the expression of the defect.

The parrot-jaw defect was observed in 34 animals in four dairy breeds: Jersey, Guernsey, Holstein, and Brown Swiss. The incisors of affected animals meet $\frac{1}{4}$ - $1\frac{1}{2}$ inches posterior to the central papilla, most commonly between the first and second dental ridges. The defect is a slight handicap to eating but has no other apparent effects.

Evidence concerning the inheritance of the defect was obtained from several sources. The condition was observed in three females in the Kansas State University Jersey herd and in two females and one bull in the Garden City Branch Station Brown Swiss herd. Experimental matings for four generations in the Jersey and Guernsey breeds and three generations or repeated backcrossing Jersey cows and their descendants to Guernsey bulls were made in the Kansas State University Dairy Genetics Project herd. These experimental matings have involved more than eighty animals.

Some study of the morphology of the defect was done on heads of animals in the experimental herd and the University Jersey and Guernsey herds. Still other information came from the measuring of 255 normal Guernsey females in eight Kansas herds.

In these herds two parrot-jaw heifers were observed. Thus, the frequency of occurrence of the defect in the Guernsey breed was estimated at 3 in 1,000.

The parrot-jaw defect in Jerseys appeared to be different morphologically from that in the other breeds. Experimental matings indicated that the inheritance of parrot-jaw in Jerseys was also different. Evidence obtained, both from experimental matings and from the Kansas State University Jersey herd, did not refute a simple recessive mode of inheritance of parrot-jaw in

this breed.

Not only did parrot-jaw in the Guernsey breed appear to be a morphologically different type from that in Jerseys, but it differed also in that it was always expressed at birth. The inheritance of the defect in this breed seemed to be more complex. Neither a dominant nor a recessive mode of inheritance satisfactorily explained all mating results. Of the two suitable epistatic gene schemes considered — dominant and recessive epistasis and duplicate recessive epistasis — the former fitted not only the pedigree information of the three related foundation animals better than did the latter, but it also better fitted the results of experimental matings.

In repeated backcrossing of Jersey cows and their descendants to parrot-jaw Guernsey bulls, dominant and recessive epistasis explained the occurrence of a normal calf from affected parents more satisfactorily than did duplicate recessive epistasis.

The results of Brown Swiss matings, like those in Guernseys, indicated a complex mode of inheritance. Although no definite mode of inheritance can be stated, single gene dominant, or recessive, inheritance can be eliminated.

Since all first generation Guernsey-Jersey and Guernsey-Holstein cross-bred animals were normal, the defect seemed to be controlled by different genes in these breeds.

In addition to the study of the inheritance, attempts were made to describe in detail the morphology of the defect in Guernseys. Numerous measurements were taken on parrot-jaw and normal heads, while intact, after butcher-skinning, and after maceration. Comparison of parrot-jaw and normal groups did not show a significant difference between groups for any measurement. However, six living parrot-jaw animals had narrower and shallower heads than did normals of comparable age. The upper jaws were longer and

the mandibles, shorter.

The comparison of butcher-skinned heads indicated that parrot-jaw heads were shallower. The distance from the poll to the angle of the mandible was shorter in parrot-jaws than in the controls, as were various measurements of jaw circumference.

The results from comparing macerated heads of parrot-jaw and normal animals were very similar to those obtained by other procedures. Macerated parrot-jaw heads were narrower and shallower than normal control heads. The maxillae and premaxillae were longer than in normal animals.

All these results indicate that the defect in Guernseys may be the result of changes in both upper and lower jaws.